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Research

Species and individual replacements contribute more than nestedness to shape vertebrate scavenger metacommunities

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Understanding the mechanisms that organize biodiversity is central in ecology and conservation. Beta diversity links local (alfa) and regional (gamma) diversity, giving insight into how communities organize spatially. Metacommunity ecology provides the framework to interpret regional and local processes interacting to shape communities. However, the lack of metacommunity studies for large vertebrates may limit the understanding and compromise the preservation of ecosystem functions and services. We aim to understand the mechanisms underlying differences in species composition among vertebrate scavenger communities – which provide key ecosystem functions, e.g. carrion consumption – within a metacommunity context. We obtained species richness and abundances at scavenger communities consuming ungulate carcasses monitored through motion-triggered remote cameras in seven terrestrial ecosystems in Spain. We partitioned beta diversity to decompose incidence-based (species presence/absence) and abundance-based dissimilarities into their components (turnover/balanced variation and nestedness/abundance gradient, respectively). We identified the environmental factors explaining the observed patterns. The vertebrate scavenger metacommunity consisted of 3101 individuals from 30 species. Changes in composition among ecosystems were mostly (> 84%) due to species or individual replacement (i.e. turnover or balanced variation). Species or individual loss/gain (i.e. nestedness or abundance gradient) accounted for 13–16% of these changes. Mean carcass weight, elevation and habitat diversity were the main factors explaining species/individual replacement. Our findings suggest that local processes such as species-sorting through habitat heterogeneity would dominate scavenger metacommunity dynamics together with stochastic forces (i.e. related to carrion unpredictability and scavenging being a widespread strategy among vertebrates). The presence of structured patterns (i.e. nestedness) in beta diversity could reflect a role of deterministic processes: mass-effects through dispersal and defaunation. Vultures are long-distance foragers and functionally dominant species, which would connect local assemblages within the metacommunity, supporting scavenger diversity and functions across space. These results highlight the importance of managing vertebrate scavenger assemblages within a metacommunity context.

Keywords: beta diversity, dispersal, scavenging ecology

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Introduction

Knowing how biodiversity organizes in space and what drivers explain its distribution across scales is central in ecology and conservation (Ricklefs 1987, Holyoak et al. 2005). Spatial biodiversity is usually partitioned into three components: local species richness (alfa diversity), regional species richness (gamma diversity) and compositional variation of the communities across sites (spatial beta diversity; Jost 2006). Because different mechanisms operate at local and regional scales to shape biodiversity, studying the relationship between local and regional diversity is essential for understanding how communities are structured (Guichard 2017). In this regard, studying beta diversity (Whittaker 1960) is a key issue to link local (i.e. alfa) and regional (i.e. gamma) diversity and to provide opportunities for the integrative management of biodiversity across spatial scales (Socolar et al. 2016).

Metacommunity theory links local and regional diversity providing a powerful framework to interpret jointly the patterns and processes that drive the organization of biodiversity across ecosystems (Logue et al. 2011). Local communities can be connected at larger (i.e. regional) spatial scales 'by the dispersal of one or more of their constituent species' forming altogether a metacommunity (Leibold et al. 2004, Mittelbach 2012). Metacommunity is, thus, a highly relevant concept in ecology and conservation as it considers species assemblages as resulting from the interaction of processes at different scales (local and regional) that were previously analysed in a separate way, which is expected to be less capable of capturing the complexity of formation and maintenance of communities (Logue et al. 2011, Guichard 2017). One of the key mechanisms that define metacommunity dynamics is the mass-effects, which implies the dispersal of organisms across heterogeneous environments away from their source habitats or communities (Leibold et al. 2004, Mittelbach 2012) and causes that dispersal rates between local communities can affect species diversity (Mouquet and Loreau 2003, Vanschoenwinkel et al. 2007). Because dispersal tends to homogenize the composition of local communities, increasing dispersal usually drives a decrease in beta diversity (Mouquet and Loreau 2003). In this work, we consider dispersal in its broader definition as the movement of individuals away from their source (Nathan et al. 2003). Accordingly, all the main ecological processes involving long-distance movements of species (e.g. foraging, natal and juvenile dispersal…) among patches are considered here as dispersal.

Besides dispersal, which acts at the larger (i.e. regional) scales, habitat heterogeneity (i.e. considered as all habitat and vegetation characteristics determining its complexity) can also drive metacommunity dynamics through species-sorting or environmental filtering, a mechanism acting at local scale and also reflected in beta diversity (Mittelbach 2012). Nonetheless, the study of metacommunities is still scarcely developed, especially for vertebrates (e.g. only 7 out of the 132, i.e. 5%, studies reported by Logue et al. 2011 dealt with vertebrate metacommunities). The underrepresentation of larger organisms (i.e. able to actively move over long distances; Soininen et al. 2007) and terrestrial systems in metacommunity analyses can have further implications regarding the understanding of biodiversity-ecosystem functioning (BEF) and -ecosystem services (BES) relationships across spatial scales. For example, large body sized species such as *Gyps* vultures are highly functional species delivering key ecosystem functions such as carrion consumption and nutrient recycling in terrestrial ecosystems where they are present (Mateo-Tomás et al. 2017). Since *Gyps* vultures can rapidly move over large areas (Ruxton and Houston 2004), they become functionally dominant species even in local communities where they are neither extant nor abundant species (Mateo-Tomás et al. 2017).

Vultures, as obligate scavengers, are specialized in rapidly locate and access carrion (Ruxton and Houston 2004) but they are not the only vertebrate scavengers. Scavenging is a widespread strategy among vertebrates, so a high diversity of species can assembly to feed on carcasses (Mateo-Tomás et al. 2015). These scavenger vertebrate communities are formed by obligate (i.e. vultures) and facultative scavengers which support key ecosystem functions and services (e.g. carrion elimination, nutrient recycling, disease control; De Vault et al. 2003). However, these important ecological processes related to scavenging have been frequently underestimated (by 16-fold in food webs; Wilson and Wolkovich 2011), thus limiting scientific and social interest on scavengers and affecting environmental conservation and management policies. The conservation and socioeconomic conflicts arisen at the beginning of the 21st century from the mismanagement of human-mediated carrion increasingly present in natural ecosystems (Oro et al. 2013, Mateo-Tomás et al. 2015) fuelled the attention of scientists and environmental managers on scavenging ecology. Livestock carcasses treated with the veterinary drug diclofenac poisoned vultures in Asia (Oaks et al. 2004), triggering rapid population declines (Green et al. 2004). Vultures were therefore replaced at carcasses by widespread facultative scavengers like dogs *Canis familiaris* and rats *Rattus* sp., which not only are less functional species regarding carcass consumption (Mateo-Tomás et al. 2017) but are also vectors of zoonotic diseases transmitted to humans (e.g. rabies; Markandya et al. 2008). Accordingly, local increases in the populations of dogs and rats resulted in higher rabies prevalence in humans, boosting health costs in countries like India (Markandya et al. 2008). In Europe, the sanitary regulations implemented in 2002 after the outbreak of bovine spongiform encephalopathy ('mad cow disease') prohibited the abandonment of livestock carcasses in the field. The resulting food shortages threatened the conservation of obligate scavengers across Europe (Tella 2001). Besides local population decreases, unusual feeding and foraging behaviours of vultures were reported, i.e. attacking livestock, feeding at garbage dumps or foraging in north-European countries outside their known distribution range (Mateo-Tomás 2009, Margalida et al. 2010).

These widespread consequences of changes in vertebrate scavenger communities across local, regional and global scales highlight the need of a better understanding of the spatial variation of diversity patterns in vertebrate scavengers. Although the patterns and processes supported by vertebrate scavenger diversity have been analysed at local and regional scales (Mateo-Tomás et al. 2015, 2017, Turner et al. 2017), no study has yet considered both scales together in a metacommunity context. Some evidence points out that vertebrate scavenger communities would be organized in a nested way (i.e. carcasses consumed by less species being a strict subset of carcasses consumed by more species; Selva and Fortuna 2007, Sebastián-González et al. 2016), and that this nestedness is related with high local species richness (i.e. alfa diversity) and ecosystem function (Sebastián-González et al. 2016). Nonetheless, the importance of these structured non-random forces (i.e. nestedness) relative to other deterministic (e.g. dispersal, habitat heterogeneity) and stochastic forces driving variation in diversity within vertebrate scavenger metacommunities remains unknown.

The current availability of multiple metrics to measure beta diversity allows differentiating between the species turnover/replacement and nestedness components of beta diversity through both pairwise and multiple-site comparisons of local species assemblages (Baselga 2010), providing new opportunities to assess these contributions in a metacommunity context. Nonetheless, although species richness and composition are key drivers of BEF/BES relationships (Cardinale et al. 2012), increasing evidence is arising on the importance of considering also species abundance as a major driver of such relationships in natural ecosystems (Winfree et al. 2015, Mateo-Tomás et al. 2017). Abundance-based decomposition of beta diversity allows thus further insights into the processes shaping species assemblages (i.e. changes in abundance) across scales, since not only pairwise but also multisite comparisons among ecosystems are recently available (Baselga 2017).

Here, we take advantage of the new approaches available to decompose beta diversity (Baselga 2017) to identify the main patterns and processes underlying biodiversity in a vertebrate scavenger metacommunity. The high dispersal abilities of vultures (e.g. home ranges > 46 000 km^2 for griffon *Gyps fulvus* and cinereous *Aegypius monachus* vultures; Morales-Reyes et al. 2016) and other facultative scavengers (e.g. juvenile dispersal distances of up to 184.3 km in golden eagles; Soutullo et al. 2006) allow considering vertebrate scavenger communities from different ecosystems in mainland Spain (i.e. ~500 000 km^2) to be connected into the same metacommunity. In fact, griffon vultures are known to forage hundreds of kilometers across Spain in a few days, while Egyptian *Neophron percnopterus*, bearded *Gypaetus barbatus* and cinereous vultures from southern Spain are frequently reported up to 600 km northwards (e.g. from Cazorla Natural Park to Cantabrian Mountains; authors unpubl., Morales-Reyes et al. 2016; Fig. 1). We analysed differences in species composition among vertebrate scavenger

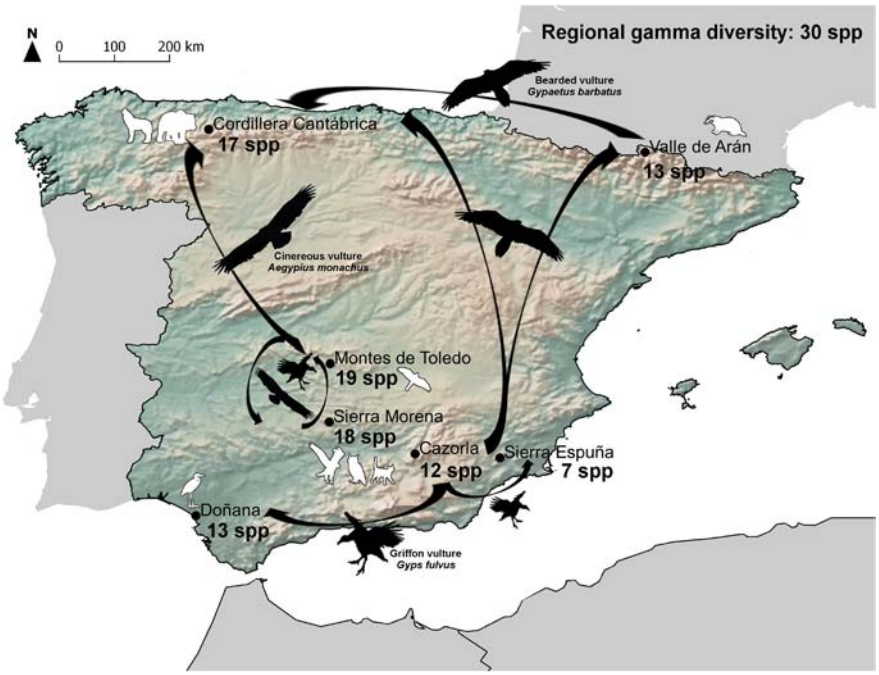

Figure 1. Vertebrate scavenger communities monitored in seven different ecosystems in mainland Spain (black dots). Black arrows exemplify some known movements of long-distance dispersers (i.e. vultures, black silhouettes) among local communities (see main text). White silhouettes depict scavengers present only in one ecosystem (i.e. from top left to bottom: wolf, bear, badger, northern goshawk, Bonelli's eagle, eagle owl, cat and cattle egret). See main text and Supplementary material Appendix 1 Table A1 and A2 for further details and the species scientific names.

communities and partitioned these compositional differences (i.e. beta diversity) to determine the relative contribution of its two main components: species turnover and nestedness (Baselga 2010) within a metacommunity context. We hypothesised that, according to the large proportion of facultative vertebrates that consume carrion worldwide (Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015), species replacement (i.e. turnover) through stochastic processes would play a major role in structuring vertebrate scavenger communities across space. Deterministic factors such as habitat heterogeneity through environmental filtering (i.e. species-sorting; Leibold et al. 2004) may promote also species turnover in community composition. Vertebrate scavenger communities seem to be structured in a nested way within communities (Selva and Fortuna 2007, Sebastián-González et al. 2016), yet it is unknown if nestedness occur among communities as well. In this regard, other deterministic forces such as anthropogenic local extinctions of large vertebrates (Wolf and Ripple 2017) and species dispersal among ecosystems (i.e. mass-effects dynamics; Leibold et al. 2004) are expected to promote nestedness among communities, e.g. through species lost or gain at larger (i.e. metacommunity) scales. According to the important role of abundance in the functioning of scavenger communities (Mateo-Tomás et al. 2017), we would assess whether species abundances follow the same spatial patterns as observed when only species identity is considered across scales.

Material and methods

Study areas and data collection

We used motion-triggered remote cameras to monitor 251 carcasses consisting of hunting remains of wild ungulate species to characterize the whole scavenger communities in seven study sites, each one representing a different ecosystem in temperate and Mediterranean mainland Spain, in 2006–2013 (Fig. 1; Supplementary material Appendix 1 Table A1). Cameras were placed near the carrion (4–8 m) just after its disposal and took pictures every 1–2 min if movement was detected both at day and night, using no glow infrared sensors to minimise disturbance. Cameras were removed after carcass consumption (i.e. only skin and bones remained). A species was considered as scavenging a carcass whenever the pictures taken provided unequivocal proof of consumption. When consumption by a species was suspected (e.g. an individual closely inspecting a carcass) but not clearly recorded, we assumed consumption whenever that species was recorded feeding on other carcasses from our study sample. Abundance per carcass was the number of individuals of a given species simultaneously appearing in the picture with the highest number of individuals of that species on that particular carcass; individuals with clearly distinct marks, fur patterns or sizes were also considered if appeared in different pictures (see Mateo-Tomás et al. 2017 for additional details).

Diversity partitioning

To understand the mechanisms underlying the differences observed among local vertebrate scavenger communities within a metacommunity context, we used additive partitioning of beta diversity among ecosystems. Incidence- and abundance-based dissimilarities provide different information on the processes driving species assemblages (Baselga 2017); thereby, we used species abundances per carcass and species richness data to perform partition analyses of beta diversity (Legendre 2014). We calculated both incidence-based (i.e. considering species presence or absence per ecosystem; Baselga 2010) and abundance-based (i.e. considering species abundance; Baselga 2013, 2017) dissimilarities. We used the Sørensen index (i.e. β_{sor}, a beta diversity measure ranging from 0, for no differentiation between assemblages, to 1, for complete differentiation) for incidence data, and its abundance-based extension (i.e. $\beta_{\%Diff}$, percentage difference; Baselga 2013, Legendre 2014). We used the R package 'betapart' (Baselga and Orme 2012) and the R functions according to Baselga (2013) to decompose both dissimilarity indices into two different components. For presence–absence data, the first component of the dissimilarity was turnover, which refers to species replacement between sites. The second was nestedness-resultant dissimilarity, characterized by the species at a site being a strict subset of the species at a richer site (Baselga 2010). Similarly, abundance-based dissimilarity decomposed into two analogous components: 1) balanced variation in species abundance (i.e. the abundance of a species declines from site 1 to site 2 in the same magnitude than the abundance of other species increases from site 1 to site 2), and 2) abundance gradient (i.e. the abundance of all species equally declines or increases from one site to another; Baselga 2013, 2017). We performed the calculations using an equal sample size per ecosystem to allow further comparisons among ecosystems, especially regarding abundance-based dissimilarity. Equal-size calculations were mean (± SD) values across 1000 runs of 11 carcasses (i.e. the number of carcasses monitored in Sierra Espuña, the ecosystem with the smallest sample; Table 1) randomly selected from the total carcasses at each ecosystem. For each run, the abundance of a species at an ecosystem resulted from adding all its individuals across the 11 carcasses resampled in that ecosystem (see Baselga and Orme 2012, and Baselga 2017 for further explanation of the 'beta.sample' function). Nonetheless, we also did the calculations using all the carcasses monitored per ecosystem. Additionally, we plotted the local contributions of each ecosystem to each one of the resulting beta diversity components (i.e. LCBD – local contributions to beta diversity – indices; Legendre 2014). These indices are comparative indicators of the ecological uniqueness of the sites within the metacommunity according to their contributions to the different beta diversity components (see Legendre 2014 for computational details). To further explore similarities between vertebrate scavenger communities in different ecosystems, we represented triangular plots of values accounting for turnover, nestedness and similarity

Table 1. Species richness and abundance of vertebrate scavenger communities in different ecosystems in mainland Spain. Sample coverage (i.e. sampled fraction of the total of individuals in the community) was calculated on abundance data (Chao et al. 2014). Obs. Observed species richness. Est. S, species richness estimated at equal sample coverage for all the study locations to compare (i.e. 99% in our analyses, S = 0.990). See Supplementary material Appendix 1 Table A1 for detailed data on species composition.

			Species richness			Species abundance	
Study area	Sample size	Sample coverage (S)	Obs.	Est. S = 0.990 (IC 95%)	Per carcass (mean ± SE)	Total	Per carcass (mean ± SE)
Cordillera Cantábrica	72	0.995	17	12 (11–13)	4 ± 0	1021	14 ± 2
Valle de Arán	15	0.98	13	16 (9–23)	3 ± 0	195	13 ± 2
Montes de Toledo	61	0.994	19	18 (15–20)	3 ± 0	634	10 ± 1
Sierra Morena	47	0.987	18	21 (14–27)	2 ± 0	375	8 ± 1
Cazorla	32	0.994	12	9 (8–11)	3 ± 0	629	20 ± 2
Sierra Espuña	11	1	7	7 (6–7)	2 ± 0	88	8 ± 2
Doñana	13	0.975	13	15 (10–20)	5 ± 0	159	12 ± 2
Total	**251**	**0.998**	**30**	**20 (19–22)**	**3 ± 0**	**31**	**11 ± 1**

(i.e. 1-dissimilarity; Podani et al. 2013) among pairs of ecosystems (Fig. 2).

We finally explored the ability of environmental factors to explain the observed patterns in the variation in scavenger species composition among ecosystems. To do this, we used distance based redundancy analysis (dbRDA; Legendre and Anderson 1999, Legendre 2014) for each component of beta diversity (incidence- and abundance-based dissimilarities, turnover/balanced variation and nestedness/abundance gradient). First, a principal coordinates analysis (PCoA) was computed for the dissimilarity, turnover/balanced variation and nestedness/abundance gradient matrices, and the principal coordinates extracted from each of them were used as response data in the dbRDAs. We used square-root

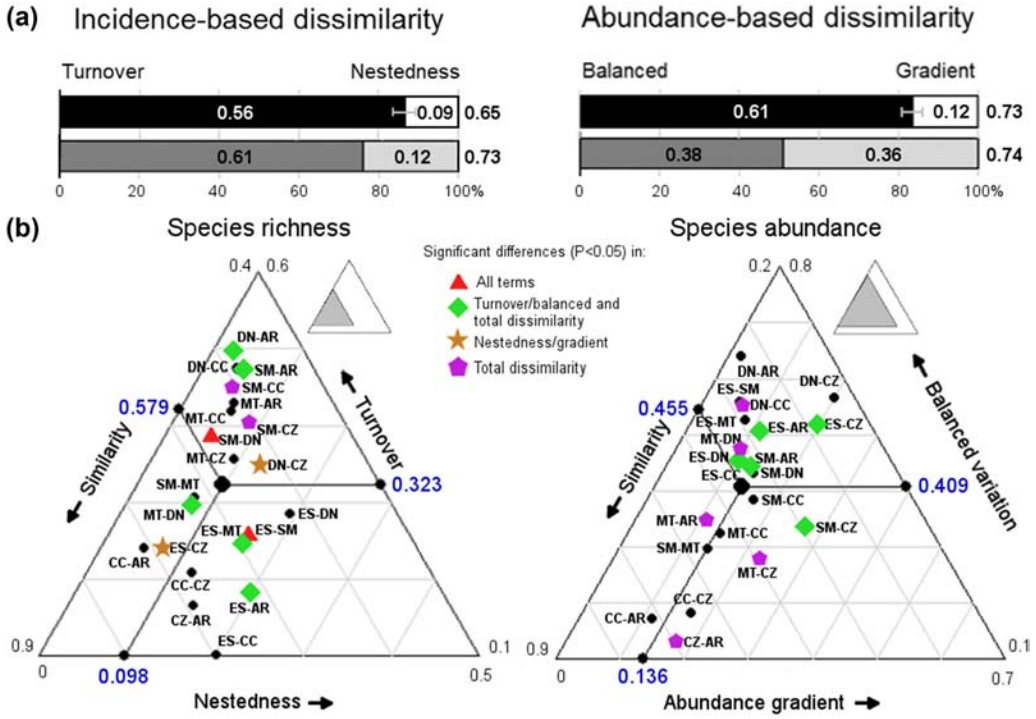

Figure 2. (a) Dissimilarity components (beta diversity) according to Baselga indices (Baselga 2010, 2013) for species richness (left panel: turnover, dark bars; nestedness, light bars) and abundance (right panel: balanced variation, dark bars; abundance gradient, light bars) among ecosystems on equal-sample size (black and white bars, n = 11) and considering all carcass per ecosystem (grey bars; see main text for further explanations). Total values (numbers) and relative contributions (% on the x axis) of the dissimilarities and their components are shown. (b) Triangular plots representing the aforementioned components of beta diversity for pairwise comparisons among ecosystems. Similarity was estimated as 1-dissimilarity. The large central dot is the centroid of the points, the smaller plots on the borders are the mean values of each component. Note different scales in each plot, as depicted by the smaller graphs at the top right. Two-letter codes identify each ecosystem as follow: CC – Cordillera Cantábrica; AR – Valle de Arán; MT – Montes de Toledo; SM – Sierra Morena; CZ – Cazorla; ES – Sierra Espuña; DN – Doñana.

transformations to reduce the non-Euclidean nature of the matrices (Legendre 2014). Environmental variables were measured at ecosystem scale (Supplementary material Appendix 1 Table A3). We considered the vertebrate species richness in each ecosystem (highly correlated with the number of bird and mammal species, $r_s = 0.94$, $p < 0.001$) as an explanatory variable of the compositional variation, since a greater vertebrate community can hold a higher number of vertebrate scavengers (Mateo-Tomás et al. 2015). Climatic variables were taken at the geographic center of each study area. We only retained mean annual precipitation per ecosystem into the analyses, since it was highly correlated with mean annual temperature and solar radiation ($r_s < -0.89$, $p < 0.007$). Other variables describing several characteristics of each carcass (e.g. weight, type, species, season when monitored) and the surrounding habitat at 10, 50 and 100-m radius (Supplementary material Appendix 1 Table A3) were averaged across monitored carcasses to obtain a single value per ecosystem. For example, elevation in each ecosystem was calculated as the average of elevation of all carcasses monitored in a given ecosystem. We retained elevation, correlated with slope ($r_s = 0.51$, $p < 0.001$), for analyses. Habitat characteristics summarizing vegetation cover at 10, 50 and 100-m radius around all carcasses within each ecosystem (Supplementary material Appendix 1 Table A3) were strongly correlated among them ($r_s > 0.75$, $p < 0.001$), so we separately considered each extent in dbRDA analyses and retained that with the highest explanatory power. We used automatic stepwise model building to select the best models in the dbRDAs (i.e. function 'ordistep' in 'vegan' package; Oksanen 2015).

We conducted Mantel tests to examine whether geographic distances between ecosystems explained beta diversity (and its components). These analyses were performed in 'vegan' package with 10 000 permutations (Oksanen 2015). All analyses were performed with the statistical programming language R (R Development Core Team).

Data deposition

Data available from Figshare Digital Repository: <https://figshare.com/s/5dbcad4ed31a0d52e3bc>.

Results

The studied scavenger metacommunity consisted of 3101 individuals from 30 vertebrate species scavenging wild ungulate carcasses in seven Spanish ecosystems (Table 1; Fig. 1). The most abundant species were the griffon vulture (1761 individuals, 56.8% of the total abundance; Supplementary material Appendix 1 Table A2), the wild boar *Sus scrofa* (247 individuals, 8.0%), the red fox *Vulpes vulpes* (245 individuals, 8.0%) and the common raven *Corvus corax* (222 individuals, 7.2%; Supplementary material Appendix 1 Table A2). The remaining species had less than 130 individuals, accounting for < 5.0% of the total abundance. Species richness across ecosystems ranged from 7 species (in Sierra Espuña) to 19 (in Montes de Toledo; Table 1; Fig. 1), averaging 14 species (± SD: 4). When all the ecosystems were standardized to an equal sample coverage (i.e. 0.990), the estimated species richness was highly correlated to the observed richness (Spearman's correlation $r_s = 0.79$, $p = 0.04$; Table 1), and positively correlated with both total vertebrate and bird and mammal species richness per ecosystem ($r_s = 0.87$, $p < 0.01$ for both). Four species (13.3% of the total, $n = 30$, species recorded; i.e. griffon vulture, red fox, wild boar and common raven) appeared in all the ecosystems (Supplementary material Appendix 1 Table A2). Eight species (26.7% of the total species recorded) were exclusively registered in only one ecosystem (Fig. 1; Supplementary material Appendix 1 Table A2).

Scavenger beta-diversity partitioning

Multi-site dissimilarities among vertebrate scavenger communities in the seven sampled ecosystems on equal-sample sizes (i.e. $n = 11$; see Methods) showed slightly lower differences for species richness (i.e. β_{sor} mean ± SD: 0.65 ± 0.02) than for species abundance ($\beta_{\%Diff}$ 0.73 ± 0.02). Changes in vertebrate scavenger richness among the seven ecosystems were mostly due to species replacement through turnover, which accounted for 87% (i.e. 0.56 out of 0.65) of the total beta diversity at ecosystem scale (Fig. 2a). Thus, nestedness (i.e. species loss or gain) only accounted for 13% (0.09) of these changes. Similarly, differences in species abundance among scavenger communities were mostly explained by individual substitution from site to site, which accounted for 84% (0.61) of total beta diversity. Abundance gradient (i.e. equivalent to nestedness in incidence-based patterns; Baselga 2013) accounted for the remaining 16% (0.12; Fig. 2a). When considering complete samples (i.e. all carcasses) per ecosystem, values for richness dissimilarity, turnover and nestedness were very akin to equal-sample sizes (Fig. 2a). Values for total abundance-based dissimilarity were also very much alike for complete samples and equal-sample sizes (i.e. 0.74 vs 0.73); yet their relative contributions of balanced variation and abundance gradient differed, as for complete samples both components equally contributed to total abundance-based dissimilarity (Fig. 2a).

Pairwise incidence-based dissimilarities in total beta diversity among ecosystems on equal-sample sizes ranged from 0.29 (Cordillera Cantábrica-Valle de Arán) to 0.51 (Valle de Arán-Doñana; mean of all pairwise comparisons = 0.42; Fig. 2b; see Supplementary material Appendix 1 Table A4 for detailed data and the results for complete samples). Species replacement (i.e. turnover) accounted for most of the pairwise comparisons between ecosystems (i.e. in 19 out of 21 comparisons, 90%, turnover values were strictly higher than nestedness values), while nestedness accounted for 10% (2 comparisons, in which nestedness values were higher than turnover ones; Supplementary material Appendix 1 Table A4). These two pairwise comparisons involved Sierra Espuña. Abundance-based pairwise dissimilarities among

ecosystem ranged between 0.28 (Valle de Arán-Cordillera Cantábrica) and 0.67 (Cazorla-Doñana; mean = 0.55; Fig. 2b, Supplementary material Appendix 1 Table A4). For abundance-based dissimilarities, replacement of individuals explained dissimilarities in 20 out of 21 comparisons (95 %) whilst abundance gradient did it for only one comparison (Supplementary material Appendix 1 Table A4).

Regarding equal-sample sizes, the geographic distance between ecosystems did not show significant correlation with the compositional variation between ecosystems in terms of total dissimilarity, turnover/balanced variation or nestedness/abundance gradient (Mantel tests, Spearman's correlation, $r_s = -0.33$ to 0.12, $p > 0.26$).

According to their local contributions to beta diversity (LCBDs), there were not large differences in species assemblages among ecosystems both considering species richness and abundance (Fig. 3). Nonetheless, Doñana and Sierra Morena were the ecosystems with the highest differences among local scavenger communities regarding species richness and abundances, respectively (Fig. 3). Doñana had the highest contribution in both species turnover and individual replacement (i.e. balanced variation). Sierra Espuña was the most exceptional site regarding nestedness and Cazorla considering abundance gradient (Fig. 3).

The resulting dbRDA explained 57.5% of the variation of the incidence-based dissimilarity between ecosystems ($F = 1.35$, $p = 0.044$). The two first axes explained 46% (first axis: 30%). The factors that explained this scavenger beta diversity were seasonal variation in carcass availability, mean elevation of the monitored carcasses and habitat diversity

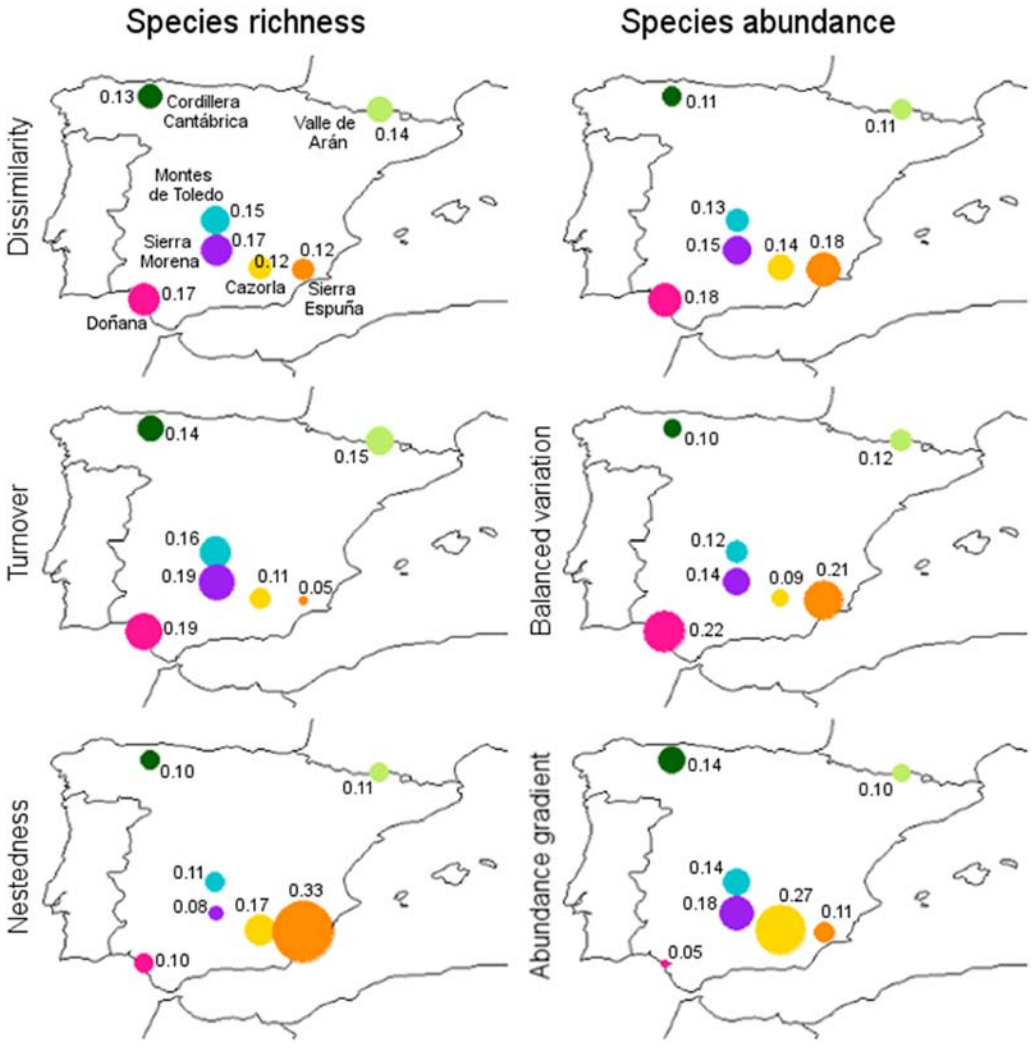

Figure 3. Ecological uniqueness of each monitored scavenger community according to its local contributions to beta diversity (LCBD show by numbers close to each point; Legendre 2014) for dissimilarity, turnover and nestedness calculated with incidence-based data (left column) and for dissimilarity, balanced variation of individuals and abundance gradient calculated with abundance-based data (right column). For dissimilarity, large points and values indicate sites with strongly different species composition (i.e. far from the multivariate centroid of the ordination graph for all the study sites; see Legendre 2014 for further computational details), for the remaining components large points and values indicate how exceptional a site is in terms of the component considered.

at 100-m radius around of the carcasses (Fig. 4). The two latter variables also explained 51% of the variation in species turnover between ecosystems (first axis: 35.6%; dbRDA: $F=2.08$, $p=0.006$; Fig. 4). dbRDA explaining nestedness did not retain any variable.

The dbRDA explained 61.0% (two first axes, 48.5%) of the variation in the abundance-based dissimilarity between ecosystems ($F=1.56$, $p=0.015$). Mean weight and mean elevation of the monitored carcasses together with habitat composition within 10-m radius around carcasses were the factors that best explained the variation (Fig. 4). Balanced variation between ecosystems was explained ($R^2=67\%$, two first axes: 56%, $F=2.03$, $p=0.008$) by the same factors than dissimilarity, but habitat diversity within 100-m radius was retained instead of habitat diversity within 10-m radius, although with a low contribution. Similarly to nestedness, the dbRDA explaining the abundance gradient did not retain any environmental variable (Fig. 4).

Discussion

Our results show that vertebrate scavenger communities across Spain are moderately different regarding their species composition in terms of both species identity and abundance (i.e. dissimilarity 0.65 and 0.73, respectively). The compositional differences (i.e. beta diversity) among ecosystems seem to be mainly due to replacement of either species or individuals rather than to structured patterns like nestedness. Our results suggest also that species replacement among vertebrate scavenger communities in a metacommunity context would be driven by habitat heterogeneity (i.e. environmental filtering or species-sorting dynamics; Leibold et al. 2004), as habitat diversity and elevation were the variables explaining turnover and balanced variation (Fig. 4).

Nestedness and abundance gradient had a low relative contribution to explain differences among scavenger assemblages (i.e. < 16%; Fig. 2) and environmental variables of their respective dbRDAs did not explain any amount of variance (Fig. 4), suggesting a limited role of these components in shaping the metacommunity. Despite this low relative contribution, the presence of these non-random patterns among communities is in accordance with previous findings on the existence of structured patterns within vertebrate scavenger communities (Selva and Fortuna 2007, Mateo-Tomás et al. 2015, Moleón et al. 2015, Sebastián-González et al. 2016). In this regard, the studied scavenger metacommunity shares a core of four vertebrate species (i.e. recorded in all Spanish ecosystems) consisting of obligate scavengers (i.e. griffon vulture) and widespread generalists (e.g. wild boar,

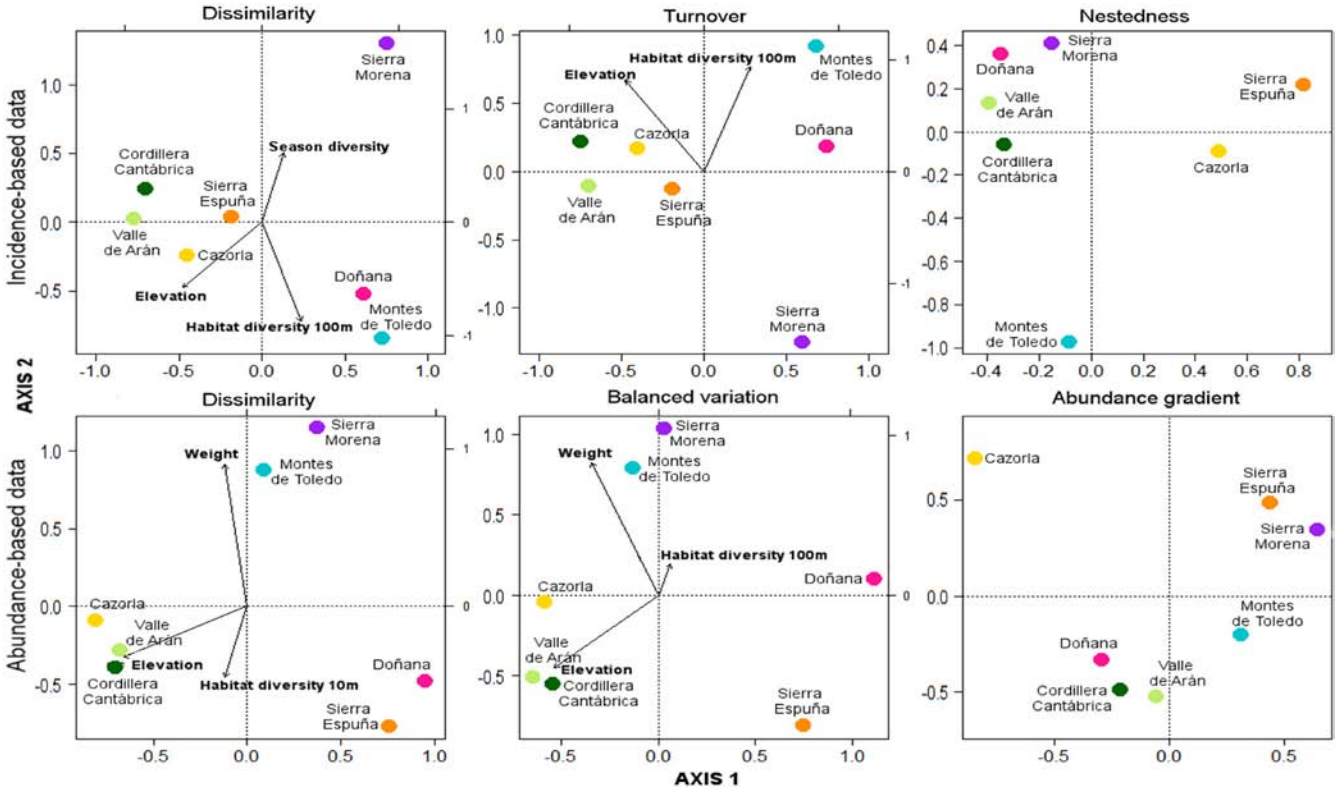

Figure 4. dbRDA plots of the dissimilarity and their components of vertebrate scavenger communities in seven Spanish ecosystems (dots). Turnover and nestedness from incidence-based data in the top row; balanced variation and abundance gradient from abundance-based data in the bottom row. Black arrows point to increasing values of the environmental variables selected by the models, with longer arrows indicating higher variable contribution. Communities located toward the end of an arrow take higher values for the environmental variable.

red fox and raven) which would promote structured assemblages through nestedness (Sebastián-González et al. 2016). Deterministic drivers, such as dispersal, may structure the metacommunity through homogenizing composition over space (Heino et al. 2015), thus favoring nestedness. The scavenger metacommunity we studied is connected at least by the dispersal of several vulture species. For example, griffon vultures – with home ranges of > 46 000 km^2 in Spain (Morales-Reyes et al. 2016) – appear in scavenger communities even in areas where they do not breed (e.g. Doñana and Sierra Espuña; Supplementary material Appendix 1 Table A2). Our analyses did not find a significant relationship between geographic distances and similarity in the composition of the Spanish vertebrate scavenger communities, likely due to vultures being long-distance foragers that may reach all the studied ecosystems and thus homogenize the scavenger communities (Vanschoenwinkel et al. 2007). Additionally, vultures can trigger facilitation processes for some facultative species to feed on carrion (Kane et al. 2014), leading to a further compositional homogenization of the scavenger assemblages. Large vulture species would play therefore a pivotal role in structuring and shaping the dynamics of the scavenger metacommunity. Our results add to the increasing body of evidence pointing out the key roles of vultures within scavenger communities not only at local (e.g. supporting important scavenger functions such as carrion consumption; Sebastián-González et al. 2016, Mateo-Tomás et al. 2017) but also at regional scales (Mateo-Tomás et al. 2015).

Other deterministic mechanisms such as historical anthropogenic factors might also explain partially the compositional differences observed among vertebrate scavenger assemblages. Several large scavenger vertebrates (e.g. Spanish imperial eagle, brown bear, Iberian wolf) have been wiped out from various ecosystems in Spain by human persecution (Wolf and Ripple 2017), thereby promoting differences among assemblages in terms of nestedness. However, despite nestedness being driven by important deterministic forces such as dispersal or defaunation, this beta-diversity component had a low relative role in structuring the scavenger metacommunity. Consequently, other deterministic (e.g. environmental filtering) and stochastic forces seem to dominate the dynamics of the scavenger metacommunity. In fact, stochasticity may play also a relevant role in driving species replacement through both the unpredictable nature of carrion and scavenging being a widespread strategy among vertebrates (Wilson and Wolkovich 2011). Both factors may randomly promote differences among vertebrate scavenger communities, as a high number of non-specialist and/or widespread scavengers (i.e. almost all carnivorous and omnivorous species) may consume this high-quality resource (Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015).

Our results allow also identifying those local vertebrate scavenger communities that disproportionally contribute to the overall beta diversity within the metacommunity context. Five out of seven ecosystems were important in maintaining incidence-based (i.e. based on species richness) beta diversity, whilst two of them contributed little to it (i.e. Sierra Espuña and Cazorla), as subsets of the other assemblages (Fig. 3). Those communities that contributed the most to beta diversity might be also functionally important sites within the metacommunity, acting as sources of long-distance foragers such as vultures within a mass-effects dynamic that would maintain vertebrate scavenging functions in other ecosystems. For example, in our study system, griffon vultures are functionally dominant species regarding carcass consumption in Sierra Espuña, an ecosystem where they do not have extant populations (Mateo-Tomás et al. 2017). Further identifying the key communities that most contribute to scavenger metacommunity dynamics would be a relevant issue from an ecological and biodiversity conservation perspective (Mouquet et al. 2013, Ruhí et al. 2017).

The similar patterns observed regarding the relative contributions of the two components of beta diversity for richness and abundance data (i.e. species/individual replacement contributed the most to changes in species diversity among ecosystems; Fig. 2), pointed out to consistent effects of the metacommunity dynamics and driving forces governing the spatial distribution of species and individuals in scavenger communities. Thus, for example, species-sorting through habitat heterogeneity (i.e. elevation and habitat diversity) would be a key driver governing not only species turnover but also the replacement of individuals of one species by others of different species (i.e. balanced variation) among vertebrate scavenger communities (Fig. 4). Nonetheless, when considering abundance data, additional factors such as carcass weight further contributed to explain differences in species diversity among communities for both total dissimilarity (i.e. beta diversity) and its balanced-variation component. Carcass size is known to affect species richness, abundance and composition of local vertebrate scavenger communities (Selva et al. 2005, Moleón et al. 2015, Turner et al. 2017). Our results would indicate a relevant role of carcass size to shape scavenger communities at larger (metacommunity) scales too. This effect would be mostly due to changes in abundance that could respond to the gregarious foraging of some vulture species that gather at large carcasses outcompeting other species (Mateo-Tomás et al. 2017). The effect of carcass characteristics on the structure and composition of scavenger communities seems to be also mediated by other factors such as habitat characteristics (Turner et al. 2017, Pardo-Barquín et al. pers. comm.). Our results provide thus additional support for species-sorting dynamics as a key mechanism shaping vertebrate diversity (through habitat heterogeneity) in the scavenger metacommunity. Furthermore, these results support also the importance of considering both species richness and abundance when analyzing the role of biodiversity in ecosystems (Winfree et al. 2015), not only at local scales (Mateo-Tomás et al. 2017) but also across scales within a metacommunity context.

Although the main objective of our work was not to assess the relative role of the different processes shaping metacommunities, our results seem to agree with the most frequently

reported metacommunity dynamics, i.e. species-sorting and mass-effects (Cottenie 2005, Logue et al. 2011). The studied vertebrate scavenger metacommunity would thus fit into a general pattern described for most metacommunities that are mainly shaped by species-sorting dynamics (e.g. through habitat heterogeneity) but also with spatial dispersal processes (i.e. mass-effects) present (Cottenie 2005). This would highlight the importance of considering spatial processes in scavenging ecology, especially when obligate scavengers (i.e. vultures) with high active dispersal abilities are present. Nonetheless, additional work is needed to properly disentangle the relative importance of these mechanisms in shaping scavenger communities across spatial scales following the main recommendations on the topic (Logue et al. 2011). In this regard, it would be useful to further assess the role of stochastic events in driving scavenger metacommunities, as this mechanism seem to has an important role in our study system and is expected to vary in a globally changing world (Logue et al. 2011). Indeed, in a scavenging context, global environmental change can alter carcass predictability through, for example, increasing human-mediated carrion (Wilson and Wolkovich 2011, Oro et al. 2013) or affecting the distribution and/or abundance of functionally dominant scavengers such as vultures or top predators (Mateo-Tomás et al. 2017).

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Supplementary material (Appendix ECOG-03854 at <www.ecography.org/appendix/ecog-03854>). Appendix 1.